Furthering knowledge on seaweed growth and development to facilitate sustainable aquaculture

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Viewpoint

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Furthering knowledge on seaweed growth and development to facilitate sustainable aquaculture.

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Paragraph 3: Early and microscopic stages of development	388		
Paragraph 4: Controlled growth and organogenesis factors: towards biomass production monitoring	332		
Paragraph 5: Current technological requirements	655		
Paragraph 6: Conclusion	267		
Acknowledgements	20		

Abstract

Macroalgae (seaweeds) are the subject of increasing interest for their potential as a source of valuable, sustainable biomass in the food, feed, chemical and pharmaceutical industries. Compared to microalgae, the pace of knowledge acquisition in seaweeds is slower despite the availability of whole-genome sequences and model organisms for the major seaweed groups. This is partly due to specific hurdles related to the large size of these organisms and their slow growth. As a result, this basic scientific field is falling behind, despite the societal and economic importance of these organisms. Here, we argue that sustainable management of seaweed aquaculture requires fundamental understanding of the underlying biological mechanisms controlling macroalgal life cycles - from the production of germ cells to the growth and fertility of the adult organisms - using diverse approaches requiring a broad range of technological tools. This viewpoint highlights several examples of basic research on macroalgal developmental biology that could enable the step-changes which are required to adequately meet the demands of the aquaculture sector.

Ecological and societal position of macroalgae

Macroalgae are macroscopic aquatic organisms belonging to three distinct and distantly-related eukaryotic lineages (commonly named green, red, and brown algae). Their unicellular ancestors diverged more than 1.6 billion years ago (Parfrey *et al.*, 2011) implying independent acquisitions of multicellularity, and leading to a bewildering diversity of life cycles, fertilization processes and morphogenetic strategies. At the ecological level, macroalgae fulfil important roles as key habitat-structuring agents and primary producers in coastal ecosystems. The goods and services seaweeds (marine macroalgae) support are varied (Figure 1), and include elevated secondary production,

nutrient cycling, energy capture and flow, and coastal defence (Steneck *et al.*, 2002). They can also significantly contribute to carbon sequestration at a level exceeding that of angiosperm marine coastal vegetation (up to 1.5 times as much as seagrass meadows, salt marshes and mangroves and up to 2% of the annual anthropogenic emission; Krause-Jensen & Duarte, 2016 and references therein). In addition, macroalgae support complex food webs in coastal zones and provide habitats and food for associated organisms, from apex predators to invertebrates (Reisewitz *et al.*, 2006). Macroalgal communities also enable transfer of biomass between ecosystems (Krumhansl & Scheibling, 2012), removal of dissolved nutrients from coastal waters and coastal protection from erosion (Arkema *et al.*, 2013). De Groot *et al.* (2012) estimated the value of coastal ecosystem services provided by macroalgae to be over 28,000 intl.$·ha^{-1}·year^{-1}.

Seaweeds are also an alternative/additional source of food, feed, fuel, biomolecules and livelihood for humans. Over 80% of macroalgal production and harvesting is at present destined for human consumption directly (Abreu *et al.*, 2014) or as hydrocolloids (thickeners, gelling agents, etc) (Rebours *et al.*, 2014). Macroalgae are also used as fertilizers and animal feed (Makkar *et al.*, 2016). In addition, the industrial sector uses seaweed biomass for nutraceuticals, cosmetics, biotechnological and pharmaceutical applications, thus propelling the growth of seaweed biotechnology (Mazarrasa *et al.*, 2013). Currently, ~28 million tonnes of seaweeds per year (wet weight) are produced and, as a proxy for the growth of the biotechnology-market of seaweed-derived products, seaweed-related patent applications increased at a rate of 11% per year since 1990 (Mazarrasa *et al.*, 2014).

While in Asia 99% of seaweed production is sourced from cultivation (accounting for 93% of the global production in 2013) (FAO, 2016), the dominant practice of non-Asian countries is still harvesting natural stocks. However, the availability of wild stocks under the current scenario of global change needs to be assessed, while management plans for seaweed exploitation must be adapted to the natural population dynamics of commercially important species. Increasing demands for high-quality seaweed biomass may therefore affect the long-term sustainability of seaweed

exploitation. Seaweed cultivation is the alternative to cope with industry's demand for biomass, concomitantly protecting natural resources (Fig. 1). Unlike terrestrial crops, they do not compete for arable land, fertilizer and freshwater resources. Furthermore, the development of Integrated Multi-Trophic Aquaculture (IMTA: co-cultivation of seaweeds with fin/shell fishes) enables recapture of excessive inorganic nutrients released in coastal areas by fish farms, thereby improving their sustainability (Holdt & Edwards, 2014). Beyond aquaculture proper, seaweed cultivation could also function as a general instrument for circular resource management (Seghetta *et al.*, 2016), treatment of waste-water produced by land-based farming and municipal treatment plants (Neveux *et al*., 2016), heavy metal biosorption (He & Chen, 2014) and recolonisation of artificial reefs (Fig. 1). As a response to this assessment, the European seaweed aquaculture sector has progressively expanded, accounting for 12% of total European biomass production in 2013 (FAO, 2016). Further expansion calls for advances in seaweed production technology, which rely on a better knowledge of both the environmental and the intrinsic factors controlling the development of macroalgae.

How could developmental biology help solve bottlenecks in seaweed aquaculture?

Mastering genetics through the control of the life cycle

Most seaweeds have complex, biphasic life cycles, involving free-living haploid gametophyte and diploid sporophyte generations (Coelho *et al.*, 2007) (Box 1). Either phase of the life cycle can be exploited, depending on the seaweed species. The harvestable biomass of kelps consists of sporophytes up to several meters long (45 m in *Macrocystis)*, while in nori (*Pyropia and Porphyra*), the life stage of interest is the haploid gametophyte. Other exploited seaweeds e.g. *Gracilaria* and *Chondrus* (red algae) have isomorphic life-cycles, with both sporophyte and gametophyte developing macroscopic exploitable thalli. Currently, clonal propagation (e.g. red alga

Kappaphycus) and recourse to a limited number of parent genotypes (kelp) account for the production of most commonly cultivated seaweeds. The resulting impoverishment of genetic diversity increases seaweed susceptibility to diseases and decreases their fitness within their cultivation environment (Loureiro *et al.*, 2015). For example, the continuous vegetative propagation of the carrageenophyte *Kappaphycus* in intensively cultivated areas has increased its vulnerability to diseases (e.g. bacterial mediated "ice-ice" disease), thereby dramatically impacting the production in various countries (Largo *et al.*, 1995). This problem requires counteraction by the selection of new breeding strains, potentially through artificial hybrids (Gupta *et al.*, 2015), but more optimally through crossings, as somatic hybridisation usually results in severe and unstable phenotypic alteration (Charrier *et al.*, 2015). However, whilst in some seaweeds the promotion of sexual reproduction still requires development (e.g. *Gracilariopsis*; Zhou *et al.*, 2013), the loss of the genetic patrimony resulting from cross-fertilisation might be detrimental to maintaining specific and valuable genotypes resulting from decades of selection. Therefore, manipulating the different steps of the seaweed life cycles would allow a balance between the maintenance of given genotypes of interest and controlled breeding. Progress in basic research opens possible paths to bypass steps of the life cycle, thereby allowing to reach this goal (Box 1).

Manipulating the sexual life cycle.

Most cultivated seaweeds reproduce sexually (kelps, red algae *Porphyra* ssp.), placing both time and genetic constraints on seaweed farmers. Physiological studies have long been establishing protocols for maintaining seaweeds in a vegetative stage or shifting them to the next phase using specific temperature and light conditions, or even by tissue ablation. This allows year-round production of juveniles and increases the cultivated net biomass (Pang & Lüning, 2004). Several illustrations of these practices applied to exploited seaweeds are displayed in Box 1. Recent fundamental studies propose potential alternatives. Treatments with algal phytohormones could be used to control the vegetative-to-reproductive transition and speed up reproduction, as illustrated in

the red alga *Grateloupia imbricata* upon addition of methyl jasmonate (García-Jiménez *et al.*, 2016).

Promoting parthenogenesis.

Other seaweeds propagate vegetatively from a single life phase through parthenogenesis, mainly by apogamy but also by apomeiosis. The flexibility is high and is a valuable feature for aquaculture, as it allows the maintenance of a specific genotype in potentially morphologically different organisms (Box 1, left side). Parthenogenesis can be induced by hybridisation (e.g. *Caloglossa* tetrasporophytes; Kamiya & West, 2008) or through chemical treatments preventing gamete motility (e.g. formaldehyde in brown algae Ectocarpales; Gwo & Chen, 1999). The lab-based identification of endogenous factors controlling seaweed parthenogenesis might provide more natural alternatives to regulate or manipulate parthenogenesis in aquaculture. Recently, Han *et al.* (2014) identified three mitochondrial proteins involved in the control of parthenogenesis in *Scytosiphon lomentaria* (brown alga Ectocarpales). In parallel, Arun *et al.* (2013) showed that algal chemical factors (so far unidentified) secreted by the parthenosporophyte of *Ectocarpus siliculosus* (brown alga Ectocarpales) control the fate of the released zoospores (Box 1). Coelho *et al.* (2011) showed that the whole parthenosporophytic stage itself was controlled by a single genetic locus. The characterisation of these factors could lead to the development of additional strategies to control parthenogenesis.

Finally, Li *et al.*, (2014) produced *Undaria pinnatifida* (brown alga) gametophytes that made only male gametes from both oogonia and antheridia (Shan *et al.*, 2015). These gametes are able to self-cross and to produce homozygous male diploid sporophytes. This example illustrates that crosses are controlled by the morphological identity of the reproductive organs rather than by their genotypes, emphasizing the importance of a control over morphogenesis.

In parallel to these improvements for seaweeds cultivated off-shore (Fernand *et al.*, 2017), standardized protocols should also be developed specifically for not-yet cultivated, high-value seaweeds amenable to on-shore cultivation. This includes seaweeds producing high-value

chemicals, or seaweeds in high demand on the food market, such as *Ulva*, *Palmaria*, *Porphyra*, *Cystoseira*, *Himanthalia*, *Codium*, *Polysiphonia* and *Asparagopsis (*Abreu *et al.*, 2014), as well as the red macroalgae *Ochtodes* and *Portieria* cultivated in photobioreactors (Rorrer & Cheney, 2004).

Altogether, basic research into the development and reproduction of macroalgae will likely provide alternative means of manipulating seaweed reproduction, which will be very valuable for future breeding programmes and aquaculture practices (Cottier-Cook *et al.*, 2016).

Early and microscopic stages of development

Seaweed growth starts with the formation and development of juveniles, which originate from the release and germination of single cells (zygotes or spores). They subsequently attach to marine substrata to initiate their sessile development (bloom-forming algae are usually free-living). Deciphering the early and microscopic developmental stages of seaweeds is an important requirement for future integrative management of their cultivation (Fig. 2). Exploitation of seaweed biomass concentrates on the macroscopic life-cycle stage, which is the sporophyte in the most predominantly exploited brown algae (*Ecklonia*, *Laminaria*, *Saccharina*, *Undaria*), together with the gametophyte in red seaweeds (*Gracilaria*, *Kappaphycus*, *Euchema*) and in some isomorphic green (*Ulva*) seaweeds. Optimizing fertilisation success could help control the rate of production of seaweed embryos in hatcheries, which, when too high, impedes the quality of sporophyte juveniles (Fig. 2 and 3). Environmental cues inducing fertility and spore/gamete release have been determined for tens of seaweed species (photoperiod, irradiance, temperature and nutrient concentration; previous section and Box 1). However, the paucity of molecular studies regarding e.g. the periodicity of gamete release, attraction of gametes to opposite sex or mating type, and cell-cell recognition (Fig. 3) stands in a stark contrast to the wealth of eco-physiological and biochemical studies that predate the molecular era. As an illustration, in certain *Ulva* species,

gametogenesis and subsequent gamete release can be artificially induced by removal of sporulation and swarming inhibitors (Vesty *et al.*, 2015 and references therein), but so far, neither these inhibitors nor the signalling pathways inducing gametogenesis have been characterised. Similar cases could be made for pheromone signalling in brown seaweeds (Boland, 1995) and glycoprotein recognition between opposite-sex gametes (Schmid *et al.*, 1994).

Many macroalgal zygotes experience polarisation prior to the growth and development of the embryo (Fig. 3), similarly to land plants and metazoans. Whether polarisation is necessary for proper development, and the identity of polarisation cues and regulatory factors, are unknown for most macroalgae: only Fucales and Dictyotales (brown algae) zygotes have allowed the identification of detailed polarisation cues (light direction and location of sperm entry; Brownlee *et al.*, 2001; Bogaert *et al.*, 2017) and of specific cell cycle checkpoints (Bothwell *et al.*, 2008). Bogaert *et al.* (2017) recently described in *Dictyota* a unique two-phase polarisation mechanism, thereby illustrating the importance of seaweeds to decipher fundamental developmental processes in the tree of life.

Controlled growth and organogenesis factors: towards biomass production monitoring,

Production of large seaweed biomass with specific features of industrial interest (polysaccharides, proteins and pigments) depends both on seaweed net growth and seaweed capacity to grow organs and tissues with specific structures and compositions. Indeed, the quantity and quality of key compounds vary within the algal body (beta-glucan in *Durvillaea*: Bobadilla *et al.*, 2013; phytohormones in *Sargassum*: Li *et al.*, 2016), and cells with thicker walls, storage organelles and vacuoles might be more resistant to dehydration, chemical exposure, eutrophication, and pathogen attacks, and hence be of high interest. Unfortunately, macroalgal cell fate specification is one of the least-understood areas of macroalgal biology. Undoubtedly, both endogenous (e.g. bacteria: Spoerner *et al.*, 2012; circadian rhythm: Cunningham & Guiry, 1989) and abiotic environmental

193 factors (light, temperature, sea currents) are required (Fig. 3), but the intrinsic signalling pathways
194 are largely unknown. To understand how to manipulate hatchery culture conditions to give
195 juveniles the best start in life in tune with aquaculture demands, additional studies assessing the
196 molecular impact of the surrounding physical and chemical environment (light, nutrients, salinity,
197 water movement) are required. In some seaweeds, complex interactions with bacteria are a
198 prerequisite for proper cell growth and differentiation into specific tissues (Goecke *et al.*, 2010).
199 This has been well-illustrated in green seaweeds (*Ulva* and *Monostroma* - Matsuo *et al.*, 2005;
200 Spoerner *et al.*, 2012), as well as in brown algal species where bacteria might control their life
201 cycle (Tapia *et al.*, 2016) and their morphology in waters with different salinities (Dittami *et al.*,
202 2014). It is tempting to hypothesize that controlling macroalgal development with bacteria will
203 direct the chemical composition of the macroalga and its value as cash crop. This is mainly relevant
204 for land-based aquaculture starting with a defined seed-stock (axenic germlings) and a synthetic
205 microbiome, which could influence the production of primary and secondary metabolites.
206 However, further work determining macroalgal-bacterial interactions throughout algal life-cycles is
207 necessary to discriminate between mutualistic, beneficial or pathogenic interactions.

208 **Current technological requirements**

209 Reliable, cost-effective and long-term maintenance of genetic resources is a major requirement to
210 ensure the sustainability of the quality of the exploited traits (biomass yield, quality of extracted
211 polysaccharides, texture and taste of species for human consumption; Chapman *et al.*, 2015). Both
212 sub-culturing of macroalgal explants and cryopreservation of macroalgal omnipotent cells are
213 current techniques to vegetatively propagate macroalgae over time. However, sub-cultivation is
214 time-consuming and re-iteration of the protocol over years is a source of bacterial or fungal
215 contamination. Long-term preservation (through refrigeration or liquid-nitrogen freezing) of
216 commercially important seaweed explants has therefore received increasing attention and several

protocols are now available. Techniques depend on the species (e.g. gametophytic filaments of *Macrocystis*; Barrento *et al.*, 2016; pieces of *Ulva* thalli; Lee & Nam, 2016; and apical meristems of *Gracilaria*: Lalrinsanga *et al.*, 2009) and a better knowledge of both the mitotic activities within the thallus and the underlying molecular mechanisms governing cell proliferation *versus* cell differentiation would accelerate the assessment of the regenerative potential of these seaweeds and the necessary development of adequate protocols (Stacey & Day, 2014) (Fig. 3). Basic research has revealed specificities in brown seaweeds, specifically in the *Fucus* embryo, where cell division is subject to distinct control mechanisms compared to other eukaryotes (Corellou *et al.*, 2001). As bacteria play a crucial role in many algal developmental processes (Goecke *et al.*, 2010), macroalgal preservation should also consider cryopreservation of algae with their natural microbiome rather than axenic explants. Therefore, development of seaweed biobanking procedures may be pivotal to meet future aquaculture demands.

Beyond cryopreservation, while some techniques are easily transferable from land plants to macroalgae, others require species-specific optimization. The impact of the sea water medium on the ionic concentration of buffers used in standard lab protocols and the different polysaccharide compositions of red and brown algal cell walls (Deniaud-Bouët *et al.*, 2014; Popper *et al.*, 2011) require different cell wall enzymolytic treatments in cytology protocols (Joubert & Fleurence, 2008). At the genetic level, the sequence of reporter genes commonly used in other organisms require modification for transgene expression, because of differing codon usages, as shown in red and green seaweeds (Uji *et al.*, 2014; Oertel *et al.*, 2015). The growing interest of the evolutionary developmental biology (“evo-devo”) community in macroalgae would help phycologists develop these techniques further.

In addition to the requirement for cell biology and genetic adjustments, ‘OMICS’ technology must be adapted to the level of analysis required to tackle developmental mechanisms taking place at the microscopic and early developmental stages (Fig. 2 and 3). Several transcriptomic (Wang *et al.*, 2015), proteomic (Qian *et al.*, 2016) and metabolomic (Kumar *et al.*, 2016 and references therein)

studies have been reported in both model and exploited macroalgae. In addition, exo-metabolomic profiling in standardized *Ulva* cultures with a designed microbiome have shown growth phase-dependent biomarkers that might be relevant for aquaculture (Alsufyani *et al.*, 2017). Such analyses are assisted by an increasing number of sequenced macroalgal genomes. Currently 18 public algal nuclear genomes have been sequenced, including four seaweeds. However, "-OMICS" studies at early developmental stages are hampered by a scarcity of tissue. While proteomics and metabolomics still require a significant biomass, transcriptomics can bypass this handicap through RNA amplification. Cell-specific expression patterns were thereby obtained using laser microdissection prior to RNA amplification on the model brown seaweed *Ectocarpus* (Saint-Marcoux *et al.*, 2015), and this technology is easily transferable to larger seaweeds.

Finally, transgenesis will be a highly valuable tool to discover how molecular processes are regulated in seaweeds, and to interfere with these processes by knocking down/upregulating endogenous genes. So far, only four multicellular algae, namely *Ulva*, *Pyropia* (*Porphyra*), *Volvox* and *Gonium* are genetically transformable (Schiedlmeier *et al.*, 1994; Oertel *et al.*, 2015; Mikami, 2014; Lerche & Hallmann, 2009), and *Ulva* is the only stably transformable seaweed (Oertel *et al.*, 2015). These first successes must now be replicated in additional, diverse species, *via* investment of time and expertise.

Conclusion

A range of protocols are available to cultivate seaweeds, thanks to previous physiological studies carried out in an applied phycological context. Building on this key achievement, practices must be refined and developed with a more focused and on-demand approach. Indeed, demand from end-users is rising for new, high-commercial potential (mainly for food) seaweeds. However, because of their low production level, these seaweeds have not received high investment so far, and as a result, no standardised cultivation and preservation protocols exist. This second big step is much

more delicate, because of the greater number of species and of their reluctance to respond to the simplest, classical protocols. The time has come, now that the first empirical studies have been carried out, to engage the community in an in-depth study of the biological processes driving the whole macroalgal life-cycle, from fertilization to the production of organisms. This must respond to end-users' expectations of robustness against environmental constraints (e.g. climate, infection, mechanical strain), biochemical composition and also natural and nature-friendly production increasingly favoured by the consumers. This is even more necessary since, despite the benefit that the development of cutting-edge technologies in animals and plants can bring to the sector, many of these technologies need to be adapted to macroalgae because of their specific ecological niche (highly saline) and their biology (in part due to their phylogenetic distance from better-known organisms). Therefore, efforts must be intensified to fill the gaps in our fundamental knowledge of macroalgal developmental mechanisms. We also believe that the scientific community of land plant researchers will benefit from a deeper understanding of seaweed developmental biology.

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Author contributions

All authors contributed to the writing of the manuscript.

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Box and Figure legends

Box 1: Life cycle stages in seaweeds and possible manipulations

Seaweed life cycles comprise several (usually 4) multicellular phases, including vegetative and fertile sporophytes and vegetative and fertile gametophytes (grey boxes). On the left, grey arrows indicate the different natural alternatives that seaweeds can use to reproduce (either sexually or asexually). On the right, brown, red and green horizontal lines represent the 3 groups of seaweeds. Transition between two successive phases, and bypassing or maintenance of one phase (either by delaying the maturation of the organism or by asexual looping) are ways to exert a tight control on the life cycle. Straight arrows indicate controls over a given phase of the life cycle (maintenance, induction or inhibition). Dashed arrows indicate asexual looping. A few specific examples are represented by the numbers that follow. [1] vertical arrow: maintaining vegetative growth of the brown seaweed *Saccharina latissima* gametophytes under red light or by sub-culturing (grinding) filaments; horizontal arrow: induction of gametophyte fertility under blue light (Luning & Dring, 1975). [2] sporulation maintenance by removal of the basal meristem of *S. latissima* (Pang & Lüning, 2004). [3] maintenance of the vegetative stage of the sporophyte: in *Porphyra* conchocelis by temperature, photoperiod and irradiance (He & Yarish, 2006); of the reproductive stage of the

sporophyte: in *Palmaria* tetrasporophytes by short daylength (Pang & Lüning, 2006). [4] control of the shift to the reproductive phase of the vegetatively propagated *Gracilariopsis* gametophyte by temperature optimisation (Zhou *et al.*, 2013). [5] identification of sporulation-inhibiting factors (Glycoprotein SP-1 and low molecular weight factor SP-2) from *Ulva* gametophytes and sporophytes (Wichard & Oertel, 2010; Vesty *et al.*, 2015). [6] parthenogenesis in brown algae (Nakahara, 1984) and red algae (*Undaria* female spore seeding; Shan *et al*., 2013). [7] production of gametophytes from gametes of the *Ectocarpus siliculosus* mutant *ouroboros* (Coelho *et al.*, 2011). [8] production of *Ulva* gametophytes from the germination of its own gametes when separated from another mating type (Wichard & Oertel, 2010). [9] germination of parthenosporophytes (instead of gametophytes in this strain) from *Ectocarpus* zoospores by an inhibiting factor produced by the parthenosporophyte (Arun *et al.*, 2013).

Figure 1: Position of macroalgae in the scientific and societal landscapes.

Macroalgae grow rapidly in a wide range of temperatures, using only sunlight, atmospheric carbon and naturally nutritious coastal waters. They are therefore valuable feedstock for the production of food, feed, biofuel, hydrocolloids, fertilisers, cosmetics, probiotics, biodegradable packaging through aquaculture and IMTA (see text for details). They provide curative ecological roles necessitated by human activities (waste-water treatments and seabed recolonisation). Ecology also benefits from a knowledge of macroalgal reproductive mechanisms *via* a better understanding of dispersion and persistence of both natural and exotic populations. This also contributes to the development of conservation protocols for threatened or susceptible populations. Because their life histories differ from land plants, macroalgae also inspire molecular evo-devo studies involving the whole green lineage.

Figure 2: Importance of the microscopic early developmental stages in the life cycle of exploited seaweeds: Example of the kelp *Saccharina latissima*.

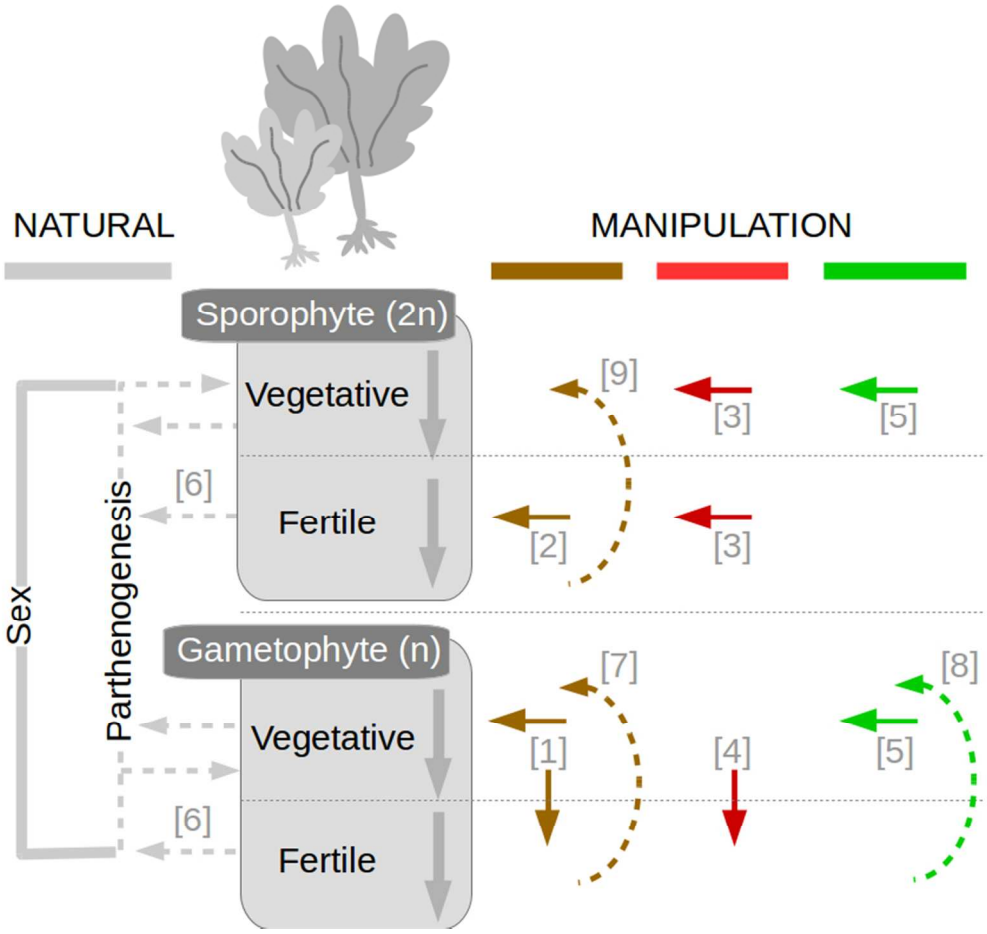
Production of kelp (large brown macroalga) sporophyte juveniles takes place in hatcheries under controlled growth conditions. Cultures of microscopic male and female gametophytes are produced from spores of macroscopic, mature plants collected from the sea. Gametophyte cultures are grown to fertility under controlled temperature and light conditions (see Box 1 for details). Microscopic, fertile, recently fertilised gametophytes, or (in turn) juvenile sporophytes are spread onto cultivation support materials (ropes or 2D substrates), which are subsequently deployed into the sea. Photos kindly provided by Teis Boderskov (Aarhus University, Denmark) and Eric Tamigneaux (Merinov, Canada).

Figure 3: Scope of beneficial outflow from basic research to seaweed aquaculture.

Sexual reproduction (top right) gives rise to polarised embryos (left), which progressively grow and differentiate, giving tissues and organs with specific shape and cellular functions (e.g. blade, stipe, holdfast, reproductive organs). The study of the different steps of the life cycle (here simplified, with adult representing either the sporophyte or the gametophyte) at the basic level (in blue) can lead to the control and improvement of key processes in seaweed aquaculture (in green). In hatcheries, density of juveniles on the cultivation support material depends on both the fertilisation rate and the adhesive potential of the embryos. Fertilisation rate itself depends on the physical interactions between the two gametes (taxis, specific recognition and membrane fusion). Better knowledge of the cell cycle and characterisation of the pluripotent cells (zygotes, meristems) will both contribute to develop cryopreservation protocols. Metabolic patterning of seaweed organs and tissues, mediated by molecular, biochemical or cellular markers, will assist farmers in

555 monitoring seaweed growth and fitness both in hatcheries and in the field. All these processes are
556 under the control of abiotic and biotic factors (see text and Box 1 for references).

Box 1



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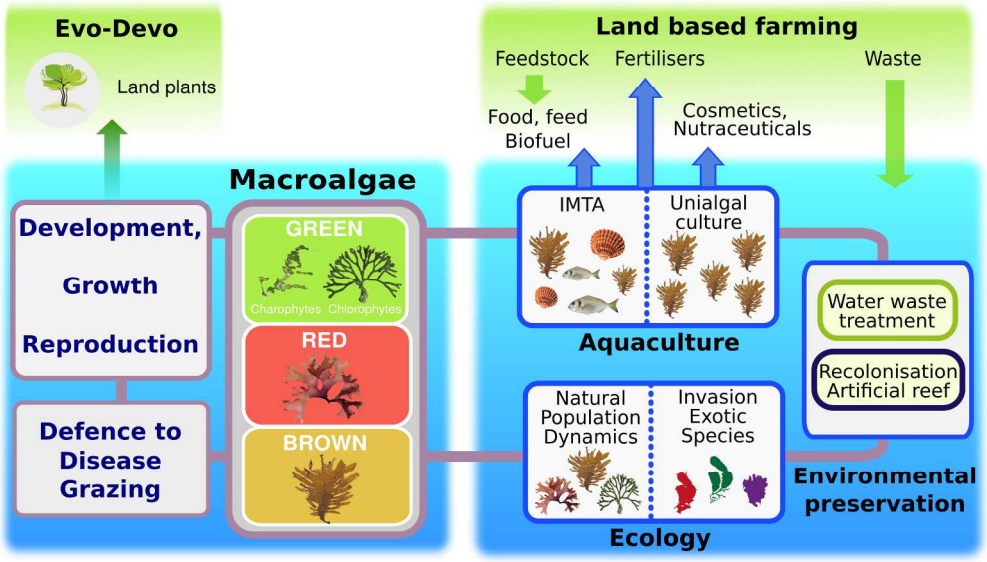

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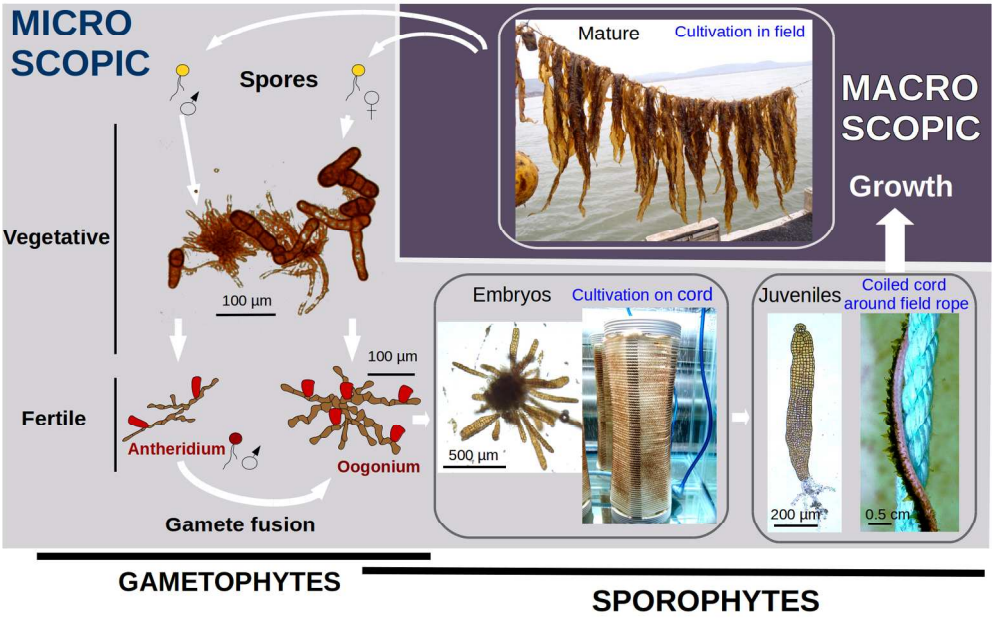
Figure 2



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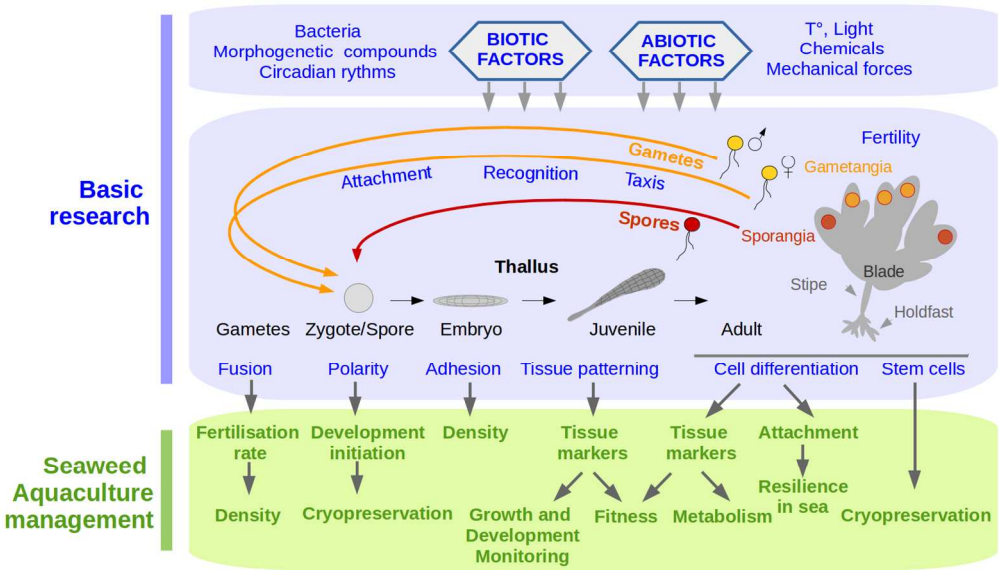

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